

Biodiversity assessment for coastal fish communities in the Baltic Sea

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Uppskattning av biologisk mångfald i fiskesamhället längs Östersjökusten

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Abstract

Biodiversity becomes of increasing concern in management of marine ecosystems. Measures of biodiversity are numerous and have been largely developed. Biodiversity can be partitioned in different components that indicate, for example, spatial and temporal changes in any communities. Coastal fish communities in the Swedish Baltic Sea have a key role in ecosystem functioning and provide many ecosystem services. Therefore, monitoring biodiversity is essential as fish communities are under anthropogenic and environmental threats. In this study, Swedish coastal fish biodiversity is assessed at different spatial and temporal levels using alpha, beta and gamma diversities. Furthermore, as size is an important trait in fish ecology and is closely related to functions, biodiversity measures have also been estimated using size-classes instead of species. While alpha and gamma diversities have higher diversity in size-class than in taxonomic classification, the opposite is observed in beta diversities. Overall, no clear spatial pattern following the north-south environmental gradient characterizing differences between areas is found, suggesting that other factors might influence biodiversity along the Swedish coast. However, beta diversities show diversity in species composition and regime dominance within area, especially in southern Sweden. Beta diversity at year level showed that coastal fish communities have been quite stable these last eleven years but with some changes. Such comparison between species- and size-based diversity provide additional information on biodiversity in the Baltic Sea and could help for management and future investigation.

Popular scientific summary

Biodiversity assessment for coastal fish communities

Human activities and environmental changes are considerable threats for species biodiversity. Coastal fish communities in the Baltic Sea play a key role in coastal ecosystems. Loss of fish biodiversity might lead to loss of ecological, economic and cultural values. For these reasons, biodiversity is of main concern in management of marine environments. Biodiversity is often expressed in terms of species, but biodiversity can also consider functional groups. Fish go across many different sizes as they grow and have different functions in the ecosystem depending on their size. But how does species biodiversity reflect functional diversity? In this project, biodiversity of coastal fish communities was measured both as species diversity and size diversity at eleven areas along the Swedish coast over eleven years, from 2005 to 2015. I found that some areas might have high species diversity and low diversity of an important functional trait, body size. Other areas might be diverse in size spectrum but not in species, showing that functional diversity does not always relate to species diversity. When looking at biodiversity at a site, diversity was generally higher in terms of size than in terms of species. On the other hand, measures of diversity between samples within an area showed that there was less variation in the functional space of an area than in its species composition, with larger differences in species than in sizes. There was also stronger changes over time in species diversity than in diversity of sizes. Overall, size diversity was more stable over time and space in comparison to species diversity, suggesting that there is more chances to find fish of same sizes in all areas and across years than of same species.

This work underlines the importance of estimating biodiversity changes and the necessity of including trait such as size in biodiversity measures. It provides a wider understanding of spatial and temporal changes that occur in fish communities in coastal ecosystems. These results could hopefully be useful for management and further investigations on coastal fish communities in the Baltic Sea.

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1 Introduction

Biodiversity is a broad topic of great importance in ecology. It has many definitions and aspects and is defined by the Convention on Biological Biodiversity (CBD) as “the variability among living organisms, covering diversity within species, between species and of ecosystems” (Heywood 1995). Biodiversity is hence of great concern when it comes to management and conservation of natural environments, both in marine and terrestrial systems. Indeed, the relationship between biodiversity and ecosystems functioning and services has been discussed and reviewed in numerous studies (Hooper *et al.* 2005, Balvanera *et al.* 2006, Cardinale *et al.* 2012, Mace *et al.* 2012). Stability and resilience of ecosystems seem to be higher in native species-rich systems (Peterson *et al.* 1998), areas of high diversity have better chance to recover from disturbances (Worm *et al.* 2006) therefore ensuring the production of services. As a result, biodiversity prevents ecosystem change and should not be omitted in management (Elmqvist *et al.* 2003). Hence, monitoring and quantifying biodiversity and its changes is a crucial aspect of management, and requires biodiversity measures that cover as many aspects of biodiversity as possible, while still being easily comparable to other ecosystems or monitoring programs.

Measures of biodiversity are usually restricted to the most classical diversity measures and are not integrated within a single unified framework, making quantitative comparison between studies rather difficult (Tuomisto 2010a). The measures of coastal fish biodiversity reported so far for the Baltic Sea only focuses on changes in α -diversity, that is, on numerical variations of diversity levels at a local scale. The problem with α -diversity measures is that they do not account for species composition but solely focus on the species abundance distribution (SAD) profile of the community. A community could be fully replaced by another, if the SAD of the new community is similar, the change would be unnoticed by measures of α -diversity. On the other hand, β -diversities are explicit measures of biodiversity changes that account for species extinction, invasion, or changes in abundances (Whittaker 1972, Tuomisto 2010a, b) and as such they are an important and missing part of the biodiversity assessment in the Baltic Sea.

One common way to study biodiversity is to look at taxonomic structure. However, species are also spatially distributed depending on their functional traits (Mouillot *et al.* 2013) and functional structure of a community is equally relevant for responses to

disturbances (Mouillot et al. 2013). Fish grow continuously through life, and such aspects are relevant trait to take into account when assessing biodiversity. Indeed, fish have distinct functions or position in the food web depending on their size (Jennings et al. 2001, Cohen et al. 2002). Their growth leads to changes in their ecological role and size can therefore be used as an indicator of their ecological function. For example, small European perch (*Perca fluviatilis*) feed on zooplankton (Koli et al. 1988) and are themselves prey to piscivorous fish such as pike (*Esox Lucius*) while large European perch (> 20cm) feed mostly on fish (Lappalainen et al. 2001) such as roach. Size variation is the result of interactions among individuals within and between species. Furthermore, some factors such as fishing are known to alter size-class distribution (Shephard et al. 2012) and therefore, some community changes might be better reflected by changes in size-class based diversity than by taxonomic-based diversity. Hence in this study, both taxonomic-based and size-class based diversity assessment will be considered.

Coastal fish communities of the Baltic Sea take a major part in total biodiversity (HELCOM 2012) and are essential to ecosystems functioning (HELCOM 2009), as they have a key role in food-web interactions (Eriksson et al. 2011, Östman et al. 2016). They are mostly local communities (Saulamo & Neuman 2002), and vary depending on environmental conditions, habitat configuration and habitat quality. In the coastal areas of the Baltic Sea, communities are characterized by a mixture of freshwater and marine species (Olsson et al. 2012). It is known that factors such as salinity, temperatures and nutrients content have a strong influence on species composition and biodiversity (Thorman 1986, HELCOM 2006, Schiewer 2008, Olsson et al. 2012, Östman et al. 2016). Patterns evidenced so far showed that species richness was decreasing with salinity and that diversity is also influenced by the high variability in temperature due to shallow waters (Thorman 1986, Schiewer 2008). There is a great pressure on coastal ecosystems and coastal fish communities, both from human activities and environmental changes (HELCOM 2009), which is today of main concern in conservation and management. Olsson et al. (2012), for example, found an increase in water temperatures and a decrease in salinity that resulted, these last years, in a decline in marine species and cold-water species, and in an expansion of freshwater fish. Such monitoring allowed them to speculate on the role of future climate variations on fish population developments. For this reason, it is of importance to assess actual trends in coastal fish

communities at different spatial scales and to investigate temporal changes across the Baltic Sea (Ådjers et al 2006, Olsson et al. 2012).

In this study, I would like to provide numerical measures of biodiversity and biodiversity changes for the Swedish coastal fish communities, hence bringing additional knowledge and clear quantification. As the Baltic Sea fish communities are expected to change according to climate or anthropogenic pressure, hopefully such knowledge can provide a numerical baseline against which these future changes could be evaluated (See Certain & Planque 2015 for a similar approach on the Barents Sea).

The aim of this study is therefore to quantify biodiversity and biodiversity changes across different areas along the Swedish Baltic coast, both in terms of taxonomic diversity and size-based diversity. The main research questions are (1) Do biodiversity assessments differ depending on whether taxonomic or size-based measures are used? (2) How do biodiversity vary across areas? (3) How do biodiversity changes, i.e. β -diversities, vary across areas? (4) Do potential differences between taxonomic- and size-based biodiversity measures vary between areas?

One hypothesis is that both assessments may differ because of size variation within species due dynamics within communities. Furthermore, these differences might vary between areas because size distribution is governed by food-web interactions (Jennings et al. 2001, Shin & Cury 2001) within local fish communities. Some changes across years are expected for each area, but these might be small as fish have long response to changes due to their longer generation. I expect different trends in biodiversity depending on the study area due to local differences in fish communities' composition and to specific environmental conditions (Thorman 1986, Olsson et al. 2012), as the areas cover a large environmental gradient, characterized by decreasing salinity towards the north (HELCOM 2006, Schiewer 2008).

2 Methods

2.1 Background

2.1.1 Biodiversity monitoring and management in the Baltic Sea

The Baltic Sea consists of a large brackish water body of 415,266 km² (Schiewer 2008) located in Northern Europe and is subdivided into five main regions: Kattegat, Baltic Proper, Gulf of Bothnia, Gulf of Finland and Gulf of Riga. One of its main

environmental characteristic is its low salinity (which also decreases from south to north) that partly explains its low biodiversity (Schiewer 2008, Elmgren 1997).

Coastal ecosystems of the Baltic Sea and its fish communities provide various ecosystem services, such as regulation of trophic structure, resilience to disturbances, food supply and recreation (Ahtiainen & Öhman 2014, Rönnbäck *et al.* 2007, Holmlund & Hammer 1999). Maintaining high biodiversity is often presented as an important objective in the Baltic Sea management strategies by the Helsinki commission (HELCOM 2007, 2009, 2012). HELCOM's Baltic Sea Action Plan (BSAP) is aiming to maintain natural abundance and composition of fish communities by reaching good environmental conditions in these coastal habitats (HELCOM 2012, 2007). Two main environmental pressures are expected to affect the coastal ecosystems in the Baltic Sea, eutrophication and climate change. Eutrophication is a major concern (HELCOM 2007, Schiewer 2008, Elmgren 2001, Snickars *et al.* 2015) and can result in changes in fish community structure and function (Ådjers *et al.* 2006, HELCOM 2006, Bergström *et al.* 2016), biodiversity (HELCOM 2009), and food web dynamics (Österblom *et al.* 2007). Climate change is also a large-scale pressure which affects ecosystems, with expecting changes in water temperature and salinity, hence coastal Baltic fish communities and fisheries might be affected in the coming future (Mackenzie *et al.* 2007).

To follow the temporal development of fish communities, monitoring has been conducted in the coastal areas of the Baltic Sea for more than fifty years, and HELCOM has coordinated regional and national monitoring programs since 2003 (HELCOM 2015). Coastal fish communities are often used as indicators to evaluate environmental and ecological status of the Baltic Sea (HELCOM 2015, Bergström *et al.* 2016). The collected data such as CPUE (catch per unit effort) are commonly used in research and coastal fish communities status has been assessed using indicators such as species diversity, size structure and trophic structure (HELCOM 2012). When diversity is estimated, it is generally described by calculating species richness, Shannon index or Simpson index.

2.1.2 Biodiversity measures

One of the most omnipresent patterns in community ecology is the species abundance distribution (SAD, Fig 1) which orders species following their abundances in the biodiversity samples and has the property of displaying a few very abundant species and many rare ones (McGill 2011). The numerical quantification of the amount of

biodiversity existing in a SAD is the purpose of diversity indices. Methods to calculate these indices are multiple and have constantly been improved since the middle of the 20th century (Magurran 2004). The first statistical developments to describe this pattern were initiated by Fisher (1943) who described the relation between species abundance and individuals' abundance using a log-series distribution. Almost simultaneously, Preston (1948) proposed the use of the lognormal distribution for the same purpose.

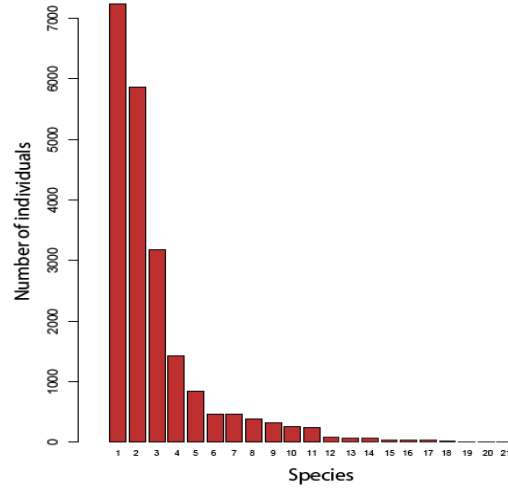


Figure 1 Example of SAD, here for fish in the Swedish coastal areas in the Baltic Sea in 2015, with species 1 corresponding to European perch (*Perca fluviatilis*).

Besides these statistical models, non-parametric metrics were also developed to describe SAD by measuring diversity, evenness or richness (McGill 2011). Their advantage was to provide numerical measures of biodiversity that was easy to understand while being free from distributional assumptions. Since then, non-parametric indices have been widely used to quantify biodiversity in ecology, such as the well-known Shannon diversity index. In a seminal paper, Hill (1973) proposed a mathematical generalization of the many non-parametric indices that had been proposed in the ecological literature. Diversity formulated as Hill's numbers is the inverse of a generalized weighted mean of the frequencies of species' abundance in a sample (Eq. 1).

$${}^qD = 1 / {}^q\bar{p}_i, \text{ with } {}^q\bar{p}_i = \sqrt[q-1]{\sum_{i=1}^S p_i p_i^{q-1}} \quad (\text{Eq. 1})$$

Hill's formula provides a diversity measure expressed in term of "effective number of species", i.e. the number of equally abundant virtual species that would provide the same diversity measure as the one seen in the sample. For communication and comparison purposes, having a diversity measure that directly relates to the concept of number of species is an advantage (Tuomisto 2010a). Other widely used indices such as

the Shannon index and the Simpson index have different measurement units: they express disorder (entropy) and probability, and albeit they correlate to diversity, they are not related to it as directly as Hill's numbers are (Tuomisto 2010a). In Hill's diversity measure, the weight given to abundant species is controlled by parameter q that ranges from 0 to $+\infty$. When $q=0$, all species have the same weight regardless of their abundance and Hill's diversity equates species richness (Hill 1973). As q increases, abundant species receive more weight over rare ones, meaning that Hill's measure focuses more on the frequency profile of the dominant species in the community. Hill's diversity connects to the Shannon index when q approaches 1, and connects to the Simpson index when $q=2$ (Hill 1973).

2.1.2.1 Biodiversity changes

While Hill was focusing on the mathematical foundations of biodiversity measures, Whittaker (1972) was modifying the way these measures would be viewed and interpreted. He introduced the distinction between α - and β -diversity that can be extracted from total diversity, i.e. γ -diversity. The α -component measures diversity within a defined unit, a sample or an area for example, while β -diversity represents diversity between units and gives, for example, a measure of temporal or spatial changes. Tuomisto (2010a, b) showed that Hill numbers could be applied to extract α - and β -diversity. Partitioning diversity has been a great development in biodiversity measurements as it became possible to investigate how diversity within and between distinct units such as communities, sites or years changes at various levels.

2.2 Study areas and fish data

For this study, fish data were obtained from the database of Coastal Fish (KUL: <http://www.slu.se/kul>), which is managed by the Department of Aquatic Resources at SLU and the Swedish Agency for Marine and Water Management. This database store fish data collected within regional and national monitoring developed within the Swedish environmental monitoring framework. Information on sampling method was taken from the monitoring program written by Karlsson (2015).

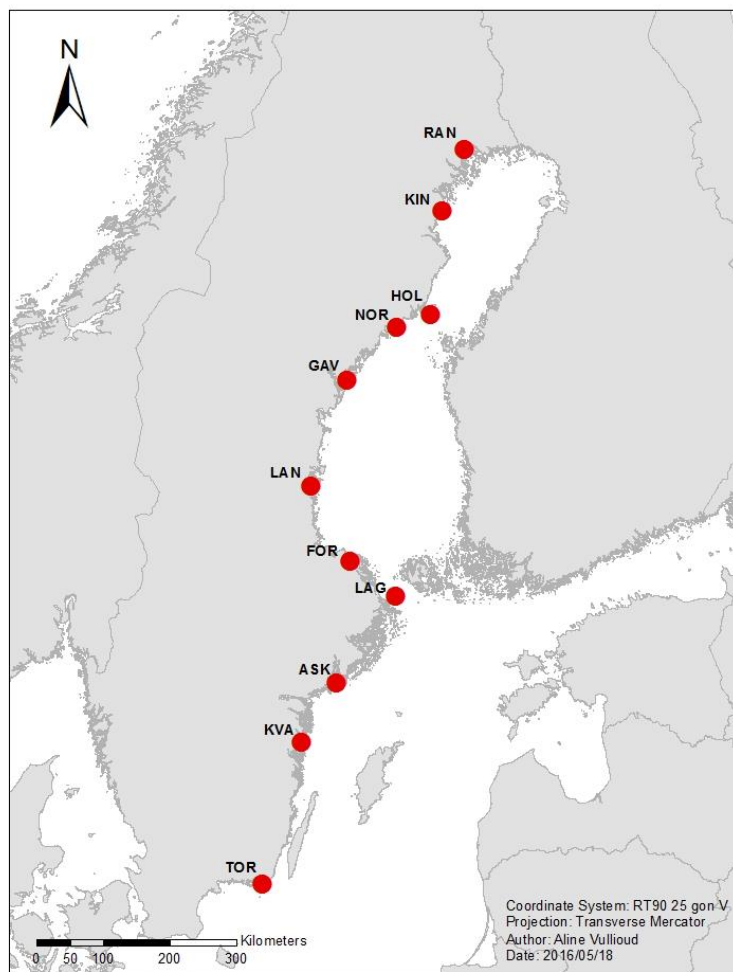


Figure 2 Eleven study areas along the Swedish east coast of the Baltic Sea.

The collection of fish abundance data is conducted in summer every year. In this study, eleven areas along the Swedish coast in the Baltic Sea were included, representing well the environmental gradient from south to north (Fig 2) (Table 1). The monitoring was initiated in 2002 in seven areas and was then extended to the whole set of areas from 2005. Sampling takes place every year, which makes it possible to study the composition of coastal fish community and its variation. In general, sampling took place in August, except for a couple of areas and years for which samples were also registered for late July and early September.

Table 1 Eleven areas were investigated. In this table, information about salinity, temperature, location, and some characteristic are described.

	Abbr.	Starting year of data collection	Salinity (psu)	Temperature (C°) during data collection	Latitude	Longitude	Situation	Nursery and recruitment
Torhamn	Tor	2002	6-8	7-23	56°7'0" N	15°47'30.0" E	Torhamn is an archipelago and coastal waters do not have much exchange with the open Sea. There is really little pollution. Natural reserves in this area are classified as Natura 2000 (Ericson et al. 2016b).	There are recruitments environments for warm-water freshwater species in the inner archipelago (Ericson et al. 2016b).
Kvädöfjärden	Kva	2002	6-8	10-25	58°1'0" N	16°46'30.0" E	Few human impacts in these coastal waters. The sampling area is conducted within nature reserve and some reserves in the surrounding are included in Natura 2000. Deep bottom but closed to open Sea.	Recruitment areas are present. There is suitable spawning ground for warm-water species such as perch, roach and pike, and cold-water species such as herring and whitefish (Ericson & Olsson 2015).
Asköfjärden	Ask	2005	3-6	10-21	58°48'42.0" N	17°43'18.0" E	There are Natura 2000 areas and nature reserves. This site is relatively deep and exposed.	The area has few spawning and nursery areas for warm-water species. There is appropriate recruitment environments for perch and pike in areas adjacent to sampling sites. Surrounded also by many spawning grounds for herring (Ericson 2014)
Lagnö	Lag	2002	5-6	10-23	59°56'9.0" N	18°80'45.0" E	This site is within a national park and many areas in the surrounding are nature reserves and Natura 2000 sites. There is some influence due to the ferries but no large emissions and pollution. (Karlsson & Ericson 2016)	Spawning and nursery areas especially for warm-water species. The southern parts of the area have also large spawning grounds for whitefish (Karlsson & Ericson 2016)
Forsmark	For	2002	3-4	10-22	60°26'1.8" N	18°09'43.8" E	Some parts of the area are classified as nature reserves. This area is quite shallow.	Species which prefer warm-water have area for recruitment in the less exposed areas, cold water species the most common in the area that have recruitment area are herring and whitefish.
Långvindsfjärden	Lan	2002	4-5	5-22	61°27'22.2" N	17°09'56.4" E	Not affected by industrial emissions and low anthropogenic influence (SLU 2013). This area is quite exposed and have good water exchange with the open sea.	Recruitment sites for herring and whitefish (SLU 2013).
Gaviksfjärden	Gav	2004	3-6	7-23	62°51'48.0" N	18°16'33.0" E	Near Natura 2000 sites and nature reserves. This area is quite steep and deep.	Many suitable spawning and nursery grounds for warm water species. This coastal area also includes a lot of recruitments environments for whitefish and herring (Hällbom 2014).
Norrbryn	Nor	2002	3-5	7-24	63°32'1.2" N	19°50'3.0" E	The bay is not receiving industrial wastewater. Some parts are included in the Natura 2000 network (Hällbom 2014). It is quite exposed.	There is few recruitment areas for perch and pike, but many for whitefish (Hällbom 2014).
Holmön	Hol	2002	3-4	11-23	63°40'53.4" N	20°52'31.2" E	Area has the status of natura 2000. Limited influence of local discharge and pollution (Ericson et al. 2016a). A lot of shallow parts.	Shallow areas are good recruitment environments for warm-water species in the area, and the more open areas are spawning grounds for whitefish (Ericson et al. 2016a)
Kinnbäcksfjärden	Kin	2004	0.5-3	8-21	65°02'48.0" N	21°31'6.0" E	Some Natura 2000 sites and nature reserves are present in the surrounding.	Next to the bay there is shallow and protected areas that are good for recruitments, especially for warm-water species. But there is also nursery grounds for whitefish and herring (Hällbom 2014).
Råneå	Ran	2002	0-2	10-25	65°49'58.2" N	22°25'34.2" E	Internal coastal waters. This site has a high incidence of sulphide, this can affect fish recruitment and explain variations in fish stocks. Rapid warming of the water in the spring and early summer in the shallow areas (Ericson 2015).	Recruitment areas for warm water species, such as perch and pike. Recruitment area for migratory fish and whitefish as well (Ericson 2015).

2.3 *Sampling method*

Fish sampling was carried out using Nordic multi-mesh gillnets. The nets were 1.8 m deep and 45 m long and fixed at the bottom. Each net was divided into 9 segments which were composed of different mesh sizes (10-60 mm). The sampling was randomized and depth-stratified (0-3m, 3-6m, 6-10m). Each site was between 400 and 3000 ha and was divided into several fishing stations that were fished by one gillnet (=one sample). There was a maximum of 45 fishing stations per area and they were randomly placed at different depths, with a minimum of 10 stations per depth interval. Each station was fished one night every year. Generally, stations that were close to each other were not fished the same night and each station were separated by at least 125 m.

Fish abundance, species, and length were recorded. In the analyses only fish with a length of 12 cm or greater were included. Indication on water temperature was also available. Longitude and latitude as well as depth were reported, in order to sample at the same station every year.

2.4 *Data preparation*

Monitoring did not start the same year for all areas (Table 1). Therefore, the analysis was limited to the time period 2005 to 2015. Sometimes, sampling was disturbed by events such as strong wind, seals or birds predation in the net. Such samples may have been biased by these interferences and were removed from the dataset prior to analysis. Between 2005 and 2015, 5871 samples (gillnets) were taken along the coastal areas. The final dataset took the shape of a $N \times S \times K$ table with N being the number of sample nets, S the number of species and K the number of size classes considered in the dataset. This became the principal dataset used for the following analysis.

2.5 *Analyses*

In this study, I mainly used the concepts and formulations provided by Whittaker (1972) and Hill (1973) to assess biodiversity. Whittaker (1972) proposed to partition total diversity γ into α - and β -diversity to describe and quantify, for instance, changes across different spatial units and time periods.

Different α - and β -diversity measures were computed to produce the biodiversity assessment. Conceptually, four measures named α -sample, β -sample, β -depth and β -year were used. Each of them measures a specific component of biodiversity or biodiversity changes (Fig 3).

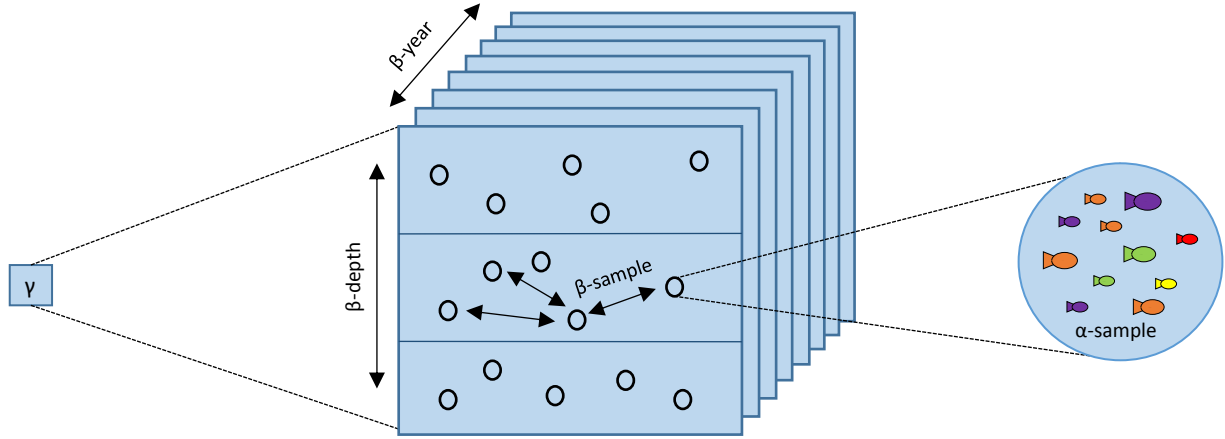


Figure 3: Conceptual figure of sampling and the type of diversity measured. One area stratified in three depth intervals and containing several gillnets (samples) which contain a certain amount of fish and this for several years. γ -diversity as total diversity of one area, α -sample as average diversity within samples within year, β -sample as diversity between samples within depth interval within year, β -depth as diversity between depth intervals within a year and β -year as average diversity between years.

In practice, Hill numbers (1973) are used to compute α - and γ -diversities, and β -diversities are deduced from their ratios at consecutive levels. This method of hierarchical partitioning of diversity, used by Certain & Planque (2015), was applied to this study to be able to investigate on coastal fish biodiversity across regions and years. Each area was analyzed separately in order to be able to compare them later on and assess spatial heterogeneity.

2.5.1 Partitioning of diversity

α - and β -diversity can be linked by a multiplicative relationship and result in γ -diversity which is the total species diversity in the dataset.

$$\alpha * \beta = \gamma \quad (\text{Eq. 2})$$

Expressed by Hill numbers, with γ expressing diversity for the whole dataset, α -diversity quantifying diversity within samples, and β -diversity between samples (Tuomisto 2010a).

$${}^qD_\gamma = {}^qD_\alpha {}^qD_\beta \quad (\text{Eq. 3})$$

And it is possible to obtain β -diversity by:

$${}^qD_\gamma / {}^qD_\alpha = {}^qD_\beta \text{ (Eq. 4)}$$

In this study, partitioning of diversity was done for each area separately taking in account three levels: samples, depth strata and years (Fig 3). As biodiversity assessment has been done independently for each area, it is important to note that herein γ -diversity is defined as the total diversity at the scale of the area and not at the regional scale. All the analyses were done with several distinct q values from 0 to 4, to adjust the weight given to dominant species and to provide a diversity profile.

2.5.2 α -diversity

The first step was to calculate α -sample, which corresponds to the average diversity within a single sample (gillnet). It is the inverse of the generalized weighted mean of all the proportional abundance of species in a sample, and can be written as follow (Tuomisto 2010a):

$${}^qD_\alpha = 1 / {}^q\bar{p}_{i|j} \text{ (Eq. 5)}$$

With ${}^q\bar{p}_{i|j}$ being the weighted mean of all the proportional abundance of species within each sample.

$${}^q\bar{p}_{i|j} = {}^{q-1}\sqrt{\sum_{j=1}^N w_j \sum_{i=1}^S p_{i|j}^q} \text{ (Eq. 6)}$$

With N the total number of samples and w_j the sample weight which represents the proportional fish abundance of sample j comparably to the whole dataset, i.e. the sum of the abundances of fish per species per gillnet divided by the total number of fish in the dataset.

2.5.3 β -diversities

From α -diversity, it was possible to extract several β -diversity values to quantify diversity between samples, between depth intervals and between years for each area, thus spatial and temporal changes and variation could be described. β -diversity measures were defined as followed (Fig 3): β -sample refers to diversity between samples within depth interval, within area, within year and is expressed as effective number of sample unit (gillnets). β -depth indicates diversity between depth intervals, within area, within year and is expressed as effective number of depth unit. β -year measures diversity between years within area, and is expressed as the effective number

of years, i.e. the number of virtual years that would have the same value of species diversity as the observed years, but entirely composed by different species.

The following relationship links all α - and β -diversities to the total γ - diversity of the dataset: to relate to γ and α diversity:

$${}^qD_\gamma = {}^qD_\alpha * {}^qD_{\beta 1} * {}^qD_{\beta 2} * {}^qD_{\beta 3} \quad (\text{Eq. 7})$$

With 1 for "sample", 2 for "depth" and 3 for "year".

2.5.4 Sample size and uncertainty

The integrated biodiversity assessment was based on bootstrapped dataset constructed by resampling. Indeed, sample size, in term of numbers of gillnets, varied between areas and between years, and it was necessary to subsample the data to make the analysis and avoid biased estimation of biodiversity due to varying sampling effort in the different study sites. Following the rarefaction approach (Magurran 2004), sample size was reduced by choosing randomly without replacement four samples for each depth interval*year*area combination. I randomly reconstructed 1000 of such subsamples, each being constituted of 1396 sample nets. Finally, the partitioning diversity analysis was done and the bootstrap enabled to extract the 95% confidence intervals together with the median. It was done by taking the 2.5% and 97.5% quantiles of the bootstrapped sampling distribution and the median of this distribution could be drawn.

It is important to note that the subsampling process suffered from some minor problems due to the survey design. Mostly, the pool of sampled gillnets available for sub-sampling could be restricted in the 6-10m depth class. Indeed, due to disturbed stations, only four of such samples were available in Forsmark and Torhamn in 2010, while only two were available in Råneå in 2008. Moreover, no samples were taken at that depth interval in Holmön at all eleven years. Hence, Holmön was subsampled only for two depth intervals, while the year 2008 was not included for Råneå in the subsampling process.

2.6 Species based diversity and Size based diversity: comparison

Once the hierarchical partitioning of diversity was done for taxonomic diversity, I applied the same framework as described above to assess diversity based on size-classes. Abundance of individuals in each size class was used to assess biodiversity. Fish were measured during data collection and classified in distinct size classes (each

centimeter was one class). In some classes, no individuals were registered. In this study, size classes were grouped 2x2 from 12 to 89 centimeters. This gave approximately the same amount of classes for size and species. One objective was to compare both assessments. Therefore, graphs of diversity profiles were created to compare both analyses. In the final synthesis graph, y-axis was containing diversity values for size-based assessment and x-axis diversity values for species based assessment which made comparison possible. One graph for each diversity measures and all q values was created. Each area was represented by a color following a gradation from blue to red corresponding to geographic position of the areas from north to south.

3 Results

3.1 Descriptive statistics

In the eleven areas, forty-two species were registered with twenty marine species, seventeen freshwater species and five brackish water species. The ten most abundant species registered in the whole dataset were European perch (*Perca fluviatilis*), Silver bream (*Abramis bjoerkna*), Bream (*Abramis brama*), Ruffe (*Cernuus*), Bleak (*Alburnus alburnus*), Roach (*Rutilus rutilus*), Smelt (*Osmerus eperlanus*), Baltic whitefish (*Coregonus maraena*), Vendace (*Coregonus albula*) and Baltic herring (*Clupea harengus*). In general, there was high abundance of fish in the range 12 to 20 centimeter, followed by 20 to 30 cm and it was rare to find fish larger than 30 cm in the sampled material.

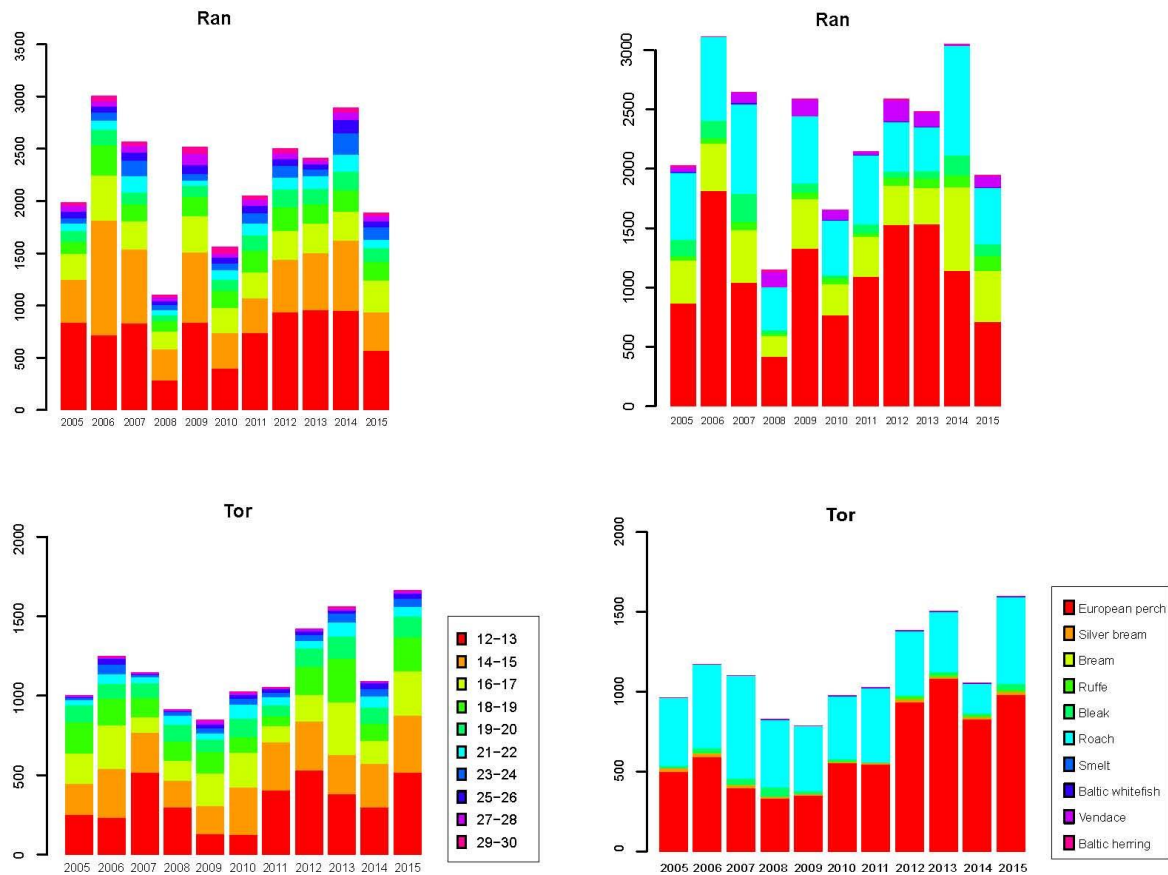


Figure 4 Example of fish abundance per size class (left) and per species (right) in Râneå and in Torhamn, the most northern and most southern study areas, showing the most common species and size class and its variation from 2005 to 2015.

3.2 Hierarchical partitioning of diversity: example of one area

The figure below (Fig 5) shows the result of the hierarchical partitioning of taxonomic diversity obtained for one area, Asköfjärden. It illustrates, for this area, that α -sample decreases rather quickly, suggesting an uneven distribution of individuals among species at the sample level. β -diversities are oscillating between 1 and 2. Among these, the “spatial” β -diversities, with β -sample that is diversity between samples within depth interval and within year (cyan) and the β -depth that is diversity between depth intervals within year (green) were the lowest, suggesting a rather homogeneous species composition over the whole sampling area. As this pattern is common across areas, estimates of β -depth and β -sample are grouped in the following sections under the term “beta sample*depth”. β -year was a bit higher, at least at low q values, showing that this area has undergone some changes in species composition through the years. However, since the β -year profile quickly drops as q increases, this suggests that these changes in community composition do not concern exclusively the most abundant species. For all profiles, confidence intervals are quite narrow, indicating a good precision of the biodiversity estimates.

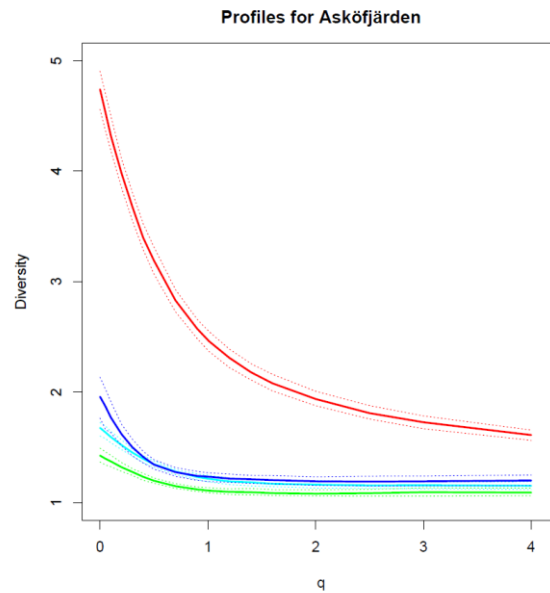


Figure 5: Example of diversity profile for one area. The thick line is the median profile across the 1000 bootstrap subsamples, while dotted lines provides the 95% confidence intervals around the profile. Red is used for α -diversity profile at the sample level. Cyan, β -diversity profile between samples. Green, β -diversity profile between depth strata. Blue, β -diversity profile between years.

3.3 Taxonomic and size based α -diversity profiles

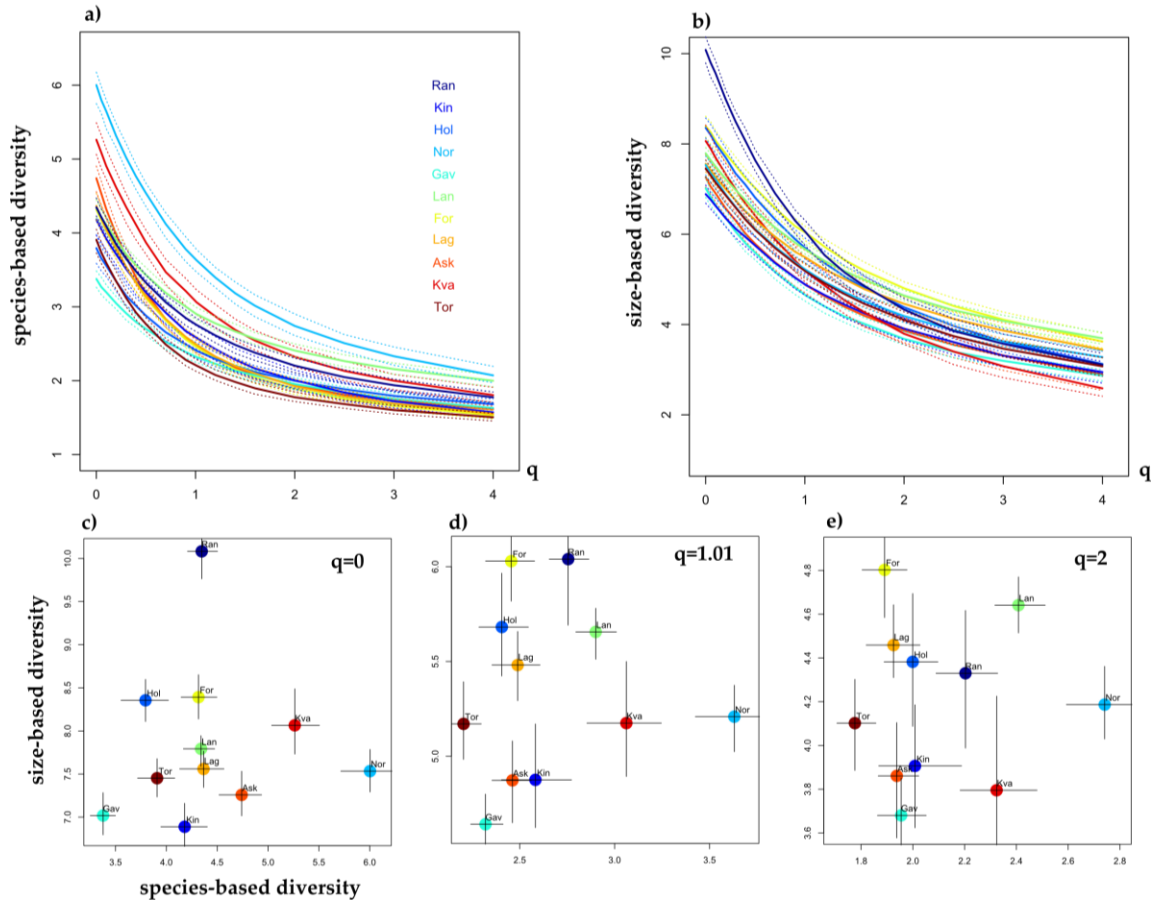


Figure 6: Taxonomic-based (a) and size-based (b) diversity profile for α -sample for all areas are represented in the two first figures. The dotted lines provides the 95% confidence intervals around the median profile. Figures c) to e) show taxonomic- and size-based diversity for $q=0$, $q=1.01$ and $q=2$ for each area. Rån: Råneå, Kin: Kinnbäcksfjärden, Hol: Holmön, Nor: Norrbyn, Gav: Gaviksfjärden, Lan: Långvindsfjärden, For: Forsmark, Lag: Lagnö, Ask: Asköfjärden, Kva: Kvädöfjärden and Tor: Torhamn.

In α -sample measures, it appears clearly that (1) α -diversity values are a little bit higher in size class diversity (Fig 6b) than species diversity (Fig 6a), (2) taxonomic profiles tend to be steeper (Fig 6a) than size class profiles (Fig 6b), suggesting that individuals in a sample are more unevenly spread across species than across size-classes and (3) there is no clear α -diversity patterns related to the north-south gradient of areas (Fig 6a-e). Furthermore, taxonomic and size-based diversity are not necessarily related. Some areas (Fig 6c; e.g. Norrbyn) have high taxonomic diversity but low size class diversity, but the opposite can also occur (Fig 6c; e.g. Råneå). Similar observations can be made for diversity values at $q=1.01$ and $q=2$ (Fig 6d, e). Differences between both assessments are not the same for all areas.

3.4 Taxonomic and size based “spatial” β -diversities

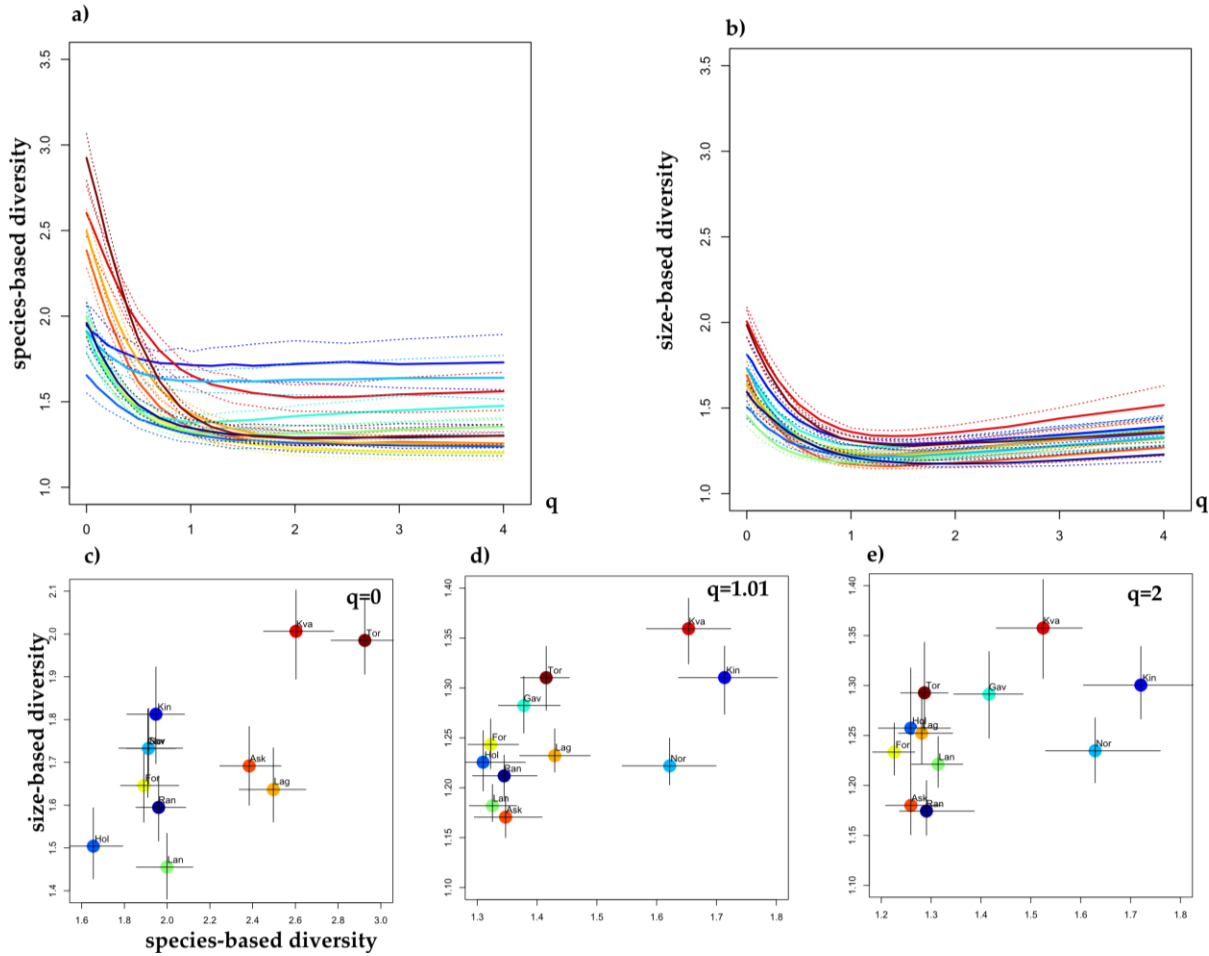
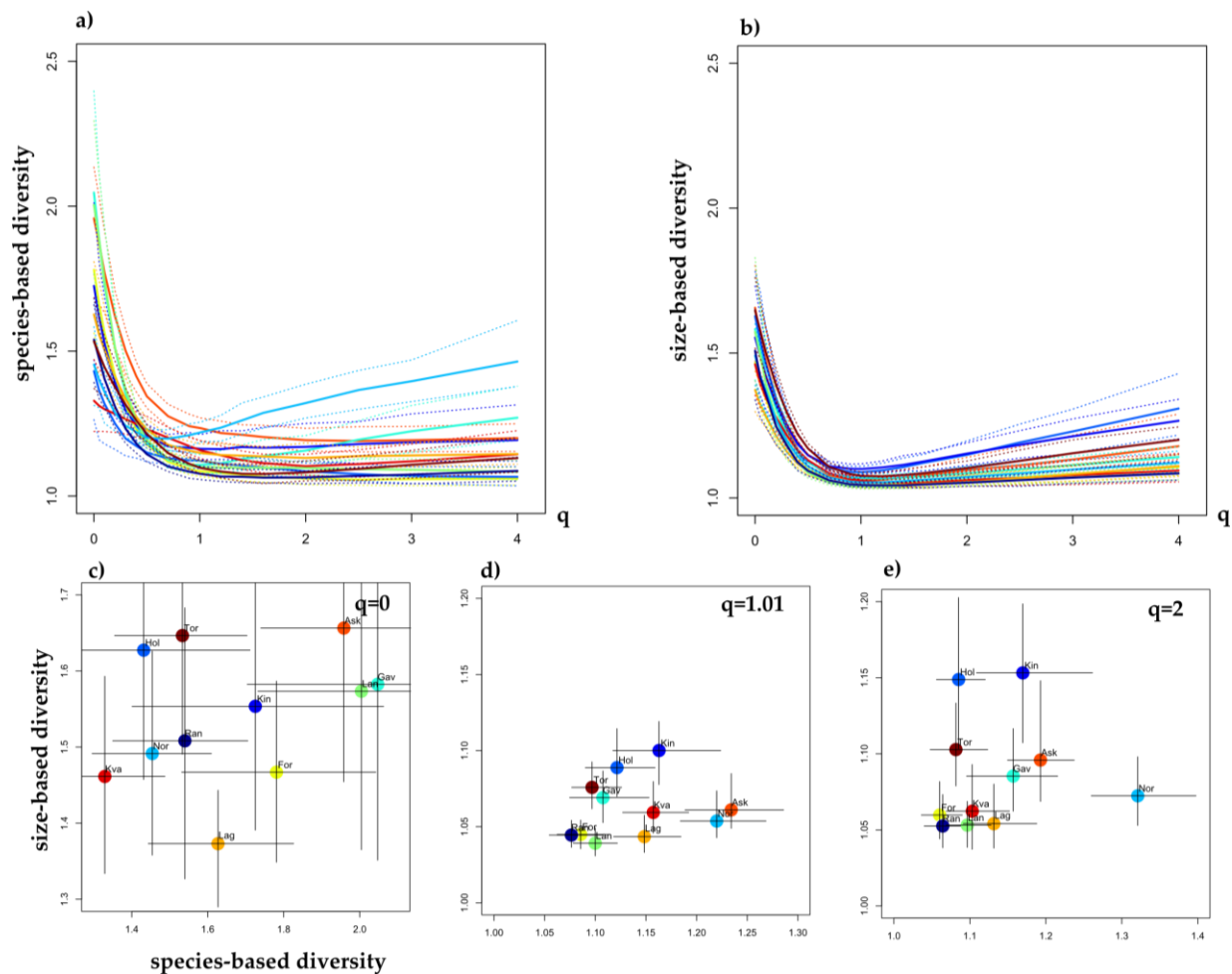


Figure 7 Taxonomic-based (a) and size-based (b) diversity profile for β -site (sample*depth) for all areas are represented in the two first figures. The dotted lines provide the 95% confidence intervals around the profile. Figures c) to e) show taxonomic- and size-based diversity for β sample*depth at $q=0$, $q=1.01$ and $q=2$ with confidence intervals.

Focusing on β -sample* β -depth, i.e. spatial diversity between samples and depth intervals within a year (Fig 7), two important patterns can be perceived. First, in the overall, spatial β -diversities are higher in taxonomic-based than in size-based measures, suggesting that between two samples of a given area, similar size classes are more likely to be found than similar species. For size-based diversity measures, β -diversity measures tend to increase again for higher q values which suggest that there are changes in size dominance regime. It is interesting to note that the profile for Kinnbäcksfjärden, in term of species-based β -site, is almost horizontal (Fig 7a), it has high β -diversity which indicates notable changes between samples both in term of species composition and dominance regime. However, this is not observed in size-

based diversity (Fig 7b). The second pattern observed is a clear difference between north and south which can be noted particularly for low q values in species based β -diversities and these contrast tend to dissipate at higher q values, meaning that differences in β -diversities between areas depends also on the weight given to dominant species (Fig 7a) and that they do not concern the most abundant species. Spatial variations between areas are more pronounced in species diversity than in size diversity.



Generally there is more variation across years in species diversity than in size class diversity, with higher β -year diversity in species based measures than in size-based measure (Fig 8a,b). Changes in diversity across years show values between 1 and 2.1 (1 means that all years are equals showing no changes). Greatest differences between years is seen when $q=0$ (Fig 8a,b), meaning some changes in species and size-class richness. However, when $q=0$ (Fig 8), there is large confidence intervals which suggests low precision for these measures. Almost no temporal changes in fish communities are seen in dominant species, i.e. when $q=1.01$ and $q=2$ (Fig 8a), except in Norrbyn. β -year diversity in terms of size-class increases from $q=1.01$ to $q=4$, in all areas, indicating that dominance regime in size class vary more these last 11 years than intermediate abundant species. Indeed, for some areas, there is a “minimum” in the profile, usually for q values between 0.5 and 1. Such minimum suggests that changes in abundance that have occurred through the years have principally concerned the most abundant species (or size class), but not the intermediate ones. This pattern is striking in Norrbyn in term of taxonomic diversity, or in Kinnbäcksfjärden and Holmön in size-class diversity. The very steep profiles are observed, suggesting that most temporal changes occur in term of species composition or size structure. Differences quickly disappear as more weight is given to species abundances. Some areas have similar profile with similar trends in size based and species based assessments but some may differ. Norrbyn and Gaviksfjärden tend to have greater changes in species diversity as $q>1.01$ than in diversity in terms of size class, while the other areas have the opposite. Not all areas have the same trends with varying q values. Northern sites have higher β -year diversity at high q values, either in size-based measures (Fig 8e; e.g. Kinnbäcksfjärden and Holmön), or taxonomic-based diversity (fig.8e; Norrbyn).

3.6 Synthesis: profiles comparison

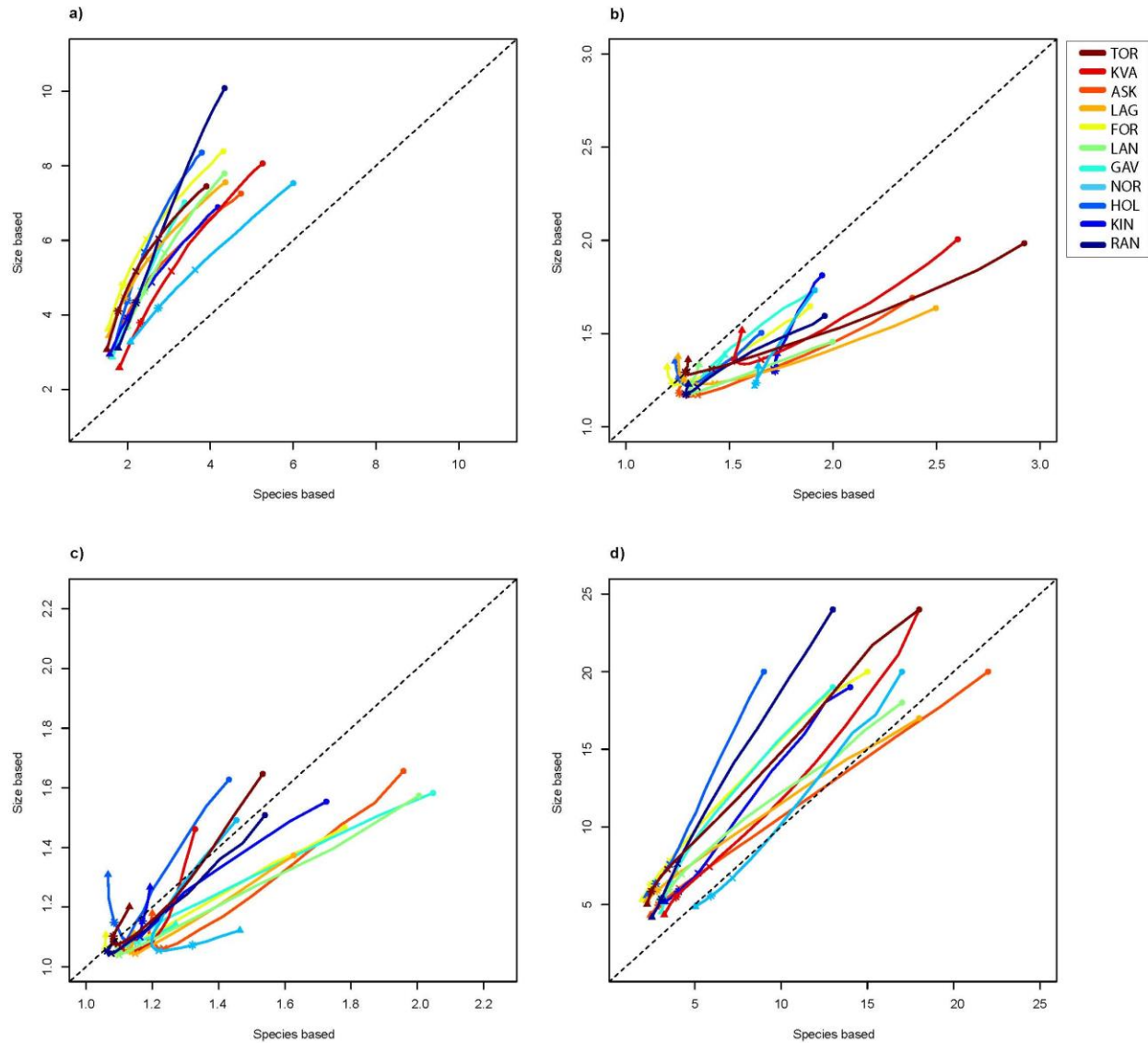


Figure 9 Graph comparing size based and species based measurements. Diversity profiles for a) α -sample, b) β - sample*depth, c) β -year and d) γ - diversity calculated at several q values from 0 to 4. Circles indicate diversity for $q=0$, cross for $q=1.01$, stars for $q=2$ and triangles for $q=4$. Each area has a different color in a gradient from red (south) to blue (north)

This figure illustrates a synthesis of the previous figures, showing the concomitant evolution of both taxonomic and size-based profiles, illustrating the most important patterns demonstrated by the analysis which are (1) differences between species based and size based diversity, (2) spatial patterns between areas, considering the environmental gradient north-south, especially in β -diversities, (3) differences between α -diversity and β -diversity. Most profiles display a straight line oriented toward the

origin, which indicates that both size-based and taxonomy-based profiles have similar steepness. “Arc” profiles observed for Norrbyn and Holmön (Fig 9c) reveal steepness divergences between the taxonomic-based and the size-based profiles. The γ diversity profiles (Fig 9d) are rather similar to the α -diversity profiles, even if differences between size-based and taxonomic-based diversities have been reduced due to the multiplication with β -diversities. Overall, there is more variation between samples and between depth intervals in terms of species than in terms of size class and the spatial variation is also more pronounced in species diversity than in size diversity. Differences between both assessments are generally the same for all areas. The figure clearly shows the most important pattern, that is, first higher size-based α -diversity (Fig 9a) and higher taxonomic-based β -diversities (Fig 9b,c). By comparing both assessments of biodiversity - species based and size based diversity - it is notable in the overall (Fig 9a-d) that a species poor area can be diverse in size class and reciprocally (Fig 9a; e.g. Råneå and Lagnö, respectively). While α -diversity and γ -diversity show higher diversity in size based assessment than species based, β -diversities show more diversity changes in species than in size class. In general, γ -diversity is higher when based on size-class than based on taxonomic classification, but the spatial differences are greater in taxonomic than size-based diversity (Fig 9d).

γ -diversity representing total diversity shows almost no spatial heterogeneity between areas in any of the two biodiversity measures with the highest q value (Fig 9d), but spatial differences can be noted, especially in species, when q is low. γ - and α -diversity show that in average, biodiversity varies between areas, but no general pattern can be found. Spatial pattern along the environmental gradient north-south is noticed in β -diversities in term of spatial taxonomic-based β -diversities (Fig 9b) with southern sites displaying more local heterogeneities in term of species composition than in term of size. Differences in biodiversity between areas depend foremost on how sensitive the measure is to dominant species, i.e. to q , and also on whether it is measured in terms of species or size-class diversity (Fig 9a,b,c,d). In contrast to γ - and α -diversity, β -diversity does not decrease uniformly with q . When $q=1.01$, there is almost no changes for both assessments with values smaller than 1.5, but there is still more variation in species composition. When $q > 2$, size class diversity increases in all areas (Fig 9b). In the overall β -year is smaller than β -sample*depth.

4 Discussion and conclusions

4.1 Size class- versus taxonomic-based assessment

The analysis revealed that taxonomic- and size-based diversity measures within Swedish coastal fish communities are not strongly related. Indeed, some areas having high size-class diversity may have low species diversity and reciprocally. Disparities between taxonomic- and size-based diversity measures were expressed differently in term of α - and β -diversity. The overall pattern is that, locally, size-class diversity is higher than species diversity but that diversity changes, and especially spatial diversity variation between samples within an area is stronger in term of taxonomic diversity than size-class diversity. It is interesting to note that this pattern was clearly evidenced for all sites. Hence, it can be concluded that whatever the species composition, a large part of the size spectra is likely covered locally by the fish community and hence no large differences in size spectra are likely to be observed from one sample to another. Size structures in fish communities have quite the same aspect in all areas along the Swedish coast. Hence, it seems that there is less variation in the functional space of an area than in its species composition.

The question if this observation is valid for any fish communities or if it is a specificity of this case study can be raised, but recent studies points towards the fact that differences between taxonomic and size-based diversities in fish may display complex patterns and do not present simple explanations as very little is known in the evolution of fish size and spatial distribution of body size with many overlapping niches (Steele & López-Fernández 2014). Individuals can share the same trophic niche by having the same prey even if they do not belong to the same species (Quintana et al. 2006), which make interactions between size classes relevant. Nevertheless, presuming that size is a proxy for function, results showed by the analysis imply that a fish community at one location provides a wide range of functions, whatever species are present, and that changes in species distribution from one location to another does not affect much the range of functions provided. This could mean that size range brings new information to the biodiversity assessment and as such it needs to be included within the diversity assessment.

Other studies (Quintana et al. 2006, Badosa et al. 2007) investigated on such comparison, using both size-based assessment and species-based assessment to describe communities' composition and dynamics in different aquatic systems and they

concluded that size-based diversity provides additional information on ecological processes in aquatic communities. Using both allow a better understanding of the dynamics, especially when communities are dominated by a few species (Quintana et al 2006). A comparison of size and species diversity in zooplankton showed that size diversity is related with biotic interaction while species diversity is more related to abiotic factors (Badosa et al. 2007). One interpretation for the pattern in this study is therefore that in the Swedish coastal fish communities of the Baltic Sea, size classes are more similar in all areas along the environmental gradient north-south because size structure is less structured by abiotic gradients than species structure. This could be a reason for finding smaller differences between areas in term of size class. Pecuchet et al. (2016) used traits to define ecological niche of a community and also underlined that traits indicate that community composition is not only influenced by abiotic drivers but also by biotic interactions.

These findings in term of functions should be considered as preliminary, and much remains to do to better characterize functional diversity for the coastal fish communities in the Baltic Coast. More functional traits need to be included, and integrated functional diversity indices based on Hill's diversity could be used (Chiu & Chao 2014). Leinster & Cobbold (2012) also suggested such method to describe species similarity to assess phylogenetic and functional diversity using a formula based on Hill numbers, just like Chao et al. (2014). These finding giving less emphasis on taxa and more on species similarity or differences in terms of functions (Chao et al. 2014) are relevant for biodiversity assessment and trait such as size could be included in these types of diversity measures. It is however interesting to compute both measures – based on size class and based on species – separately to be able to compare them and extract the trends for each independently. One methodological issue might also be that size is a continuum variable and sizes are grouped in distinct classes and depending on the chosen range of size classes, the diversity might be different for the same community (Ruiz 1994). Functional distance should also be calculated between size-classes to give more accurate results on functionality (Leinster & Cobbold 2012).

4.2 North-south gradient in term of biodiversity

γ - and α -diversity do not show any clear spatial patterns following the environmental gradient involving variation in water temperatures, decreasing salinity from south to north as it could be expected. These results indicate that spatial variation in biodiversity between areas is not so obvious and simple and others factors might be involved.

On the other hand, β -site measures show heterogeneity in species composition in all areas. β -sample*depth shows that variation of species within area is higher in sites in the south than in the north of Sweden. This variation is especially pronounced in species diversity in the south at low q value and also in the north at high q value. This shows that the north-south diversity gradient previously evidenced in the fish coastal community by Olsson *et al.* (2012) & Ådjers *et al.* (2006) for example, might result from higher diversity changes between samples in term of species composition, as α -diversities are fairly similar along the north-south gradient, but the “spatial” β -diversities are not. This indicates that local heterogeneities in communities’ composition are higher in the most southern sites. One next step to understand this pattern would be to link these β -diversity measures to measures of habitat heterogeneity, to understand if the signature observed in the β -diversities are driven by the underlying landscape and habitats. If not, this means that other processes must be advocated such as maybe differences in species movement patterns, with species more actively moving and mixing with others in the most northern areas, therefore lowering “spatial” β -diversities.

One parameter influencing species composition could be the configuration of the coastal areas. Composition might vary depending on the shallowness of waters and the exchange waters with the open Sea; depending if it is an inner archipelago, an area opened or closed to the open Sea. Indeed, the Swedish coastline is long and the habitats are various depending on environmental and geological conditions (Schiewer 2008). All study areas are coastal waters and almost all of them are not directly influenced by human impact and are within protected areas (Table 1). As previously seen (Thorman 1986, HELCOM 2006, Schiewer 2008, Olsson *et al.* 2012), factors such as water temperature, salinity and connection to open waters might influence fish communities and should be further investigated to see if any significant correlation with the biodiversity measures. Therefore, it would be interesting also to see how environmental and physical variables may be statistically related with these biodiversity measurements.

4.3 Temporal biodiversity changes for the coastal fish community

Temporal changes have been noted in this study as in many others studies, significant changes in species abundance and composition in coastal fish communities occur in the Baltic Sea through long time periods (Ådjers *et al.* 2006, Bergström *et al.* 2016, Ojaaver *et al.* 2010, Olsson *et al.* 2015, Köster *et al.* 2003). These developments are generally area-

specific depending on different environmental factors (Olsson et al. 2015). However, in this study, temporal change is represented by numerical diversity values, i.e. β -year. The results of the analysis revealed some temporal changes in biodiversity but these have not been very strong over the monitored period, suggesting a good stability of the coastal fish community of the Baltic Coast. As seen in β -year, changes both in size structure and species composition are minors. One explanation could be that eleven years' time period is not long enough long to investigate on changes in fish communities that may take longer time to have clear drift in their composition or to see drastic change in biodiversity. Some sites such as Norrbyn displayed significant temporal changes in dominance regime, which could be explained by the increase in smelt and decrease in perch, for example (Fig 10). But such regime changes were not noted in size-classes. But overall temporal variability in community composition was lower than the "spatial" variation for most sites.

Changes in fish communities could be amplified in future years as salinity and temperature might changes with ongoing climate change (Genner et al. 2010, Olsson et al. 2012, MacKenzie et al. 2007) as well as the impact on species diversity and size diversity (Collie & Rochet 2010). For these reasons, such measures as β -year are really informative and it would be interesting to look at in the coming future monitoring and compare to previous assessments.

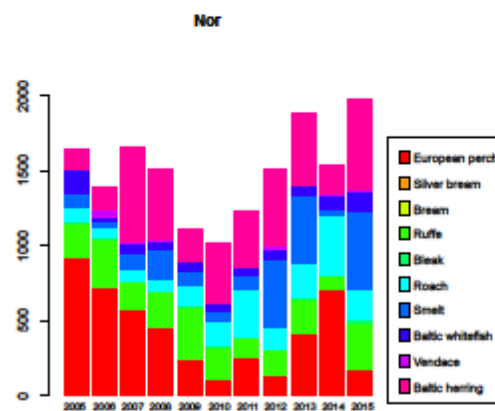


Figure 10 Barplots showing changes in dominant species composition these last eleven years in Norrbyn.

4.4 Extending this biodiversity assessment: going further?

The present study laid the first steps of what could become a general use for the assessment of fish biodiversity in the Baltic Sea. This application could be improved in a large number of ways. First, it would be interesting to extend these results to the whole Baltic coast, to see if evidenced pattern in term of α -and β -diversity remains the same when studied over a larger scale. Second, explicit distance in both size-based and taxonomic-based community compositions between areas should be quantified and linked to the actual geographical distance between sites, in order to reveal some indication on areas connectivity. Third, the whole statistical framework could be updated to produce a biodiversity assessment that integrates species function explicitly through an extensive species*traits matrix, including traits such as size, trophic level, age, etc. Lastly, additional information regarding the environmental characteristics of each areas should be included as well, in order to link the observed patterns of diversity and diversity changes with their potential drivers, hence increasing the ability to predict the fate of diversity under changing pressure scenarios.

4.5 Conclusions

By partitioning biodiversity in its several components, it was possible to see how species composition and size structure vary between and within areas, and across years. Size-based biodiversity and species-based biodiversity showed different trends in all diversity measures. Coastal fish diversity varies between areas even if no strong pattern, following the environmental gradient characterized by decreasing salinity and different local climate, were found. These assessments could be used as a reference for future investigation on biodiversity along the coastal areas of the Baltic Sea and could be extended to a larger scale. Secondly, these findings show an explicit link to function and ecological processes within the coastal fish communities that explicitly address questions regarding ecosystem services. This information may be useful for current and future management. One further research based on these biodiversity measurements could be the estimation of the provision of an ecosystem service such as recreational fishing by using methods of valuing and quantifying this service by assessing fishers preferences in term of fish size catch to obtain sociological information regarding the production of a service across monitored sites on the Baltic Coast.

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